Semicircular canal size and locomotion in colobine monkeys: a cautionary tale

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ABSTRACT

The semicircular canals of the inner ear are the organ of balance, tracking head rotation during movement and facilitating stabilisation of vision. Morphological characteristics of the canals are correlated with agility scores related to locomotion. To date, however, the relationship between canal morphology and specific locomotor behaviours, such as leaping, is unclear. Knowledge of such a relationship could strengthen the inferences of locomotion of extinct taxa. To test this, crania of two sets of closely related primate species (*Presbytis melalophos* and *P. potenziani*; *Colobus guereza* and *C. polykomos*) that differ in the percentage of leaping in their locomotor repertoire were examined using microscopic computed tomography (μCT). Three-dimensional virtual models of the bony labyrinth were derived and the radius of curvature of each of the three canals was evaluated relative to cranial size. The findings are contradictory; one leaping form (*P. melalophos*) differs from its congener in possessing significantly larger lateral canals, a pattern seen in previous studies of primates, while the other leaper (*C. guereza*) has significantly smaller posterior canals than its close relative. These results undermine efforts to determine specific locomotor behaviours from the bony labyrinth of extinct primates.

48 INTRODUCTION

49

50 Locomotor studies of primates focus primarily on the postcranial evidence (e.g., Su and Jablonski,
51 2009). Hard and soft tissue characteristics generally associated with habitual locomotor modes are
52 found in the limbs (Fleagle, 1976, 1977), although non-locomotor activity also affects the
53 postcrania (Dunham et al., 2015). More recently, however, the advent of modern imaging
54 techniques has allowed the examination of the internal portions of the cranium, including the
55 labyrinth of the temporal bone, which includes the organ of balance (Spoor & Zonneveld, 1998).
56 Exploration of the link between labyrinth morphology and motion has yielded substantial results,
57 both within primates and among mammals more generally (Spoor et al., 2007; Welker et al., 2009;
58 Billet et al., 2012; Pfaff et al., 2015).

59

60 The inner ear (Fig. 1) is comprised of numerous connected cavities known as the osseous (or bony)
61 labyrinth in mammals (Gray, 1908; Spoor & Zonneveld, 1995, 1998; Schmelzle et al. 2007; Welker
62 et al., 2009; Billet et al., 2012; Gunz et al., 2012; Pfaff et al., 2015) and other vertebrates (Boistel et
63 al., 2011). The bony labyrinth consists of the cochlea, vestibule and semicircular canals
64 (Sinnatamby, 2006), in which are contained the components of the membranous labyrinth: cochlea
65 duct, the sac-like utricle and saccule, and the semicircular ducts, respectively (Gray, 1908;
66 Sinnatamby, 2006; Walker et al., 2008). The cochlea houses the hearing system, while the vestibular
67 system (vestibule and semicircular canals) forms the organ of balance. These systems reside within
68 the otic capsule of the petrosal portion of the temporal bone (Lieberman, 2011).

69

70 Figure 1 about here

71

72 The membranous labyrinth is smaller in diameter (lumen) than the enclosing osseous labyrinth, and
73 is separated from the bony wall by a supporting fluid known as perilymph (Ekdale, 2013). The

membranous labyrinth contains fluid known as endolymph (Spoor, 2003; Sinnatamby, 2006), a heavy gelatinous fluid (Gibson, 1968) that responds to rotational acceleration of the head with a corresponding deflection, which in turn moves the hair-like cilia inside the semicircular ducts proportionally to the force of the turn; the corresponding signal is transmitted to the brain via the vestibulocochlear nerve (Gibson, 1968; Mather, 2009). The semicircular canals (and the ducts within them) are orientated in roughly orthogonal planes; thus, the brain interprets rotary head movement through a combination of input in three different axes: pitch, roll and yaw (Walker et al., 2008). It is the membranous labyrinth that determines the crucial factors for balance sensitivity (e.g., size of the semicircular ducts), but as these variables are difficult or impossible to determine after death, characteristics of the bony canals alone are used in studies of the relationship between labyrinth morphology and locomotion (Spoor, 2003).

Figure 2 about here

At a relatively wide scale, placental mammal species that move in ways that include quicker and more active actions require changes in the semicircular canals of the inner ear to cope with the more extensive head movement these taxa experience (Spoor et al. 2007; Ryan et al., 2012). This mammalian pattern has been proposed for primates, as well; for example, forms that habitually leap (e.g., galagos, tarsiers) are reported to have relatively large semicircular canals, especially the lateral (Spoor et al. 2007). For this finding to be operationalised with respect to fossil taxa, however, it is necessary to demonstrate that similar and/or closely related taxa that differ in locomotor pattern also differ significantly in bony labyrinth morphology, particularly as some extant primates have been shown to deviate from expectation (Spoor et al., 2007). The hypothesis that *Colobus* possesses larger canals than *Procolobus* because the former leaps more frequently (Walker et al., 2008) is taken as the starting point of the present investigation.

To test the prediction that closely related colobines differ in their semicircular canal morphology due to differences in the percentage of travel time spent leaping, an important part of the typical colobine locomotor repertoire (Davison, 1982), two members of the genus *Colobus* (*C. polykomos*, *C. guereza*) and the genus *Presbytis* (*P. melalophos* and *P. potenziani*) that differ in the percentage of leaping in their overall locomotor repertoire (Table 1) are examined here. To support the hypothesis that larger canals are associated with leaping, it is expected that both species pairs will show the same relationship (i.e., the leaping form in each genus will have larger canals than its congener).

All four of the taxa examined here are medium sized (6-13kg) arboreal monkeys with a high percentage of leaves in the diet (Rowe, 1996; Fleagle, 1999). *P. melalophos* and *P. potenziani* live on the SE Asian islands of Sumatra and Mentawai, respectively, although *P. melalophos* is also found on the mainland of the Malay Peninsula (Fleagle, 1999). The difference in their degree of leaping behaviour is not obviously related to their habitats, as both species inhabit primary and secondary forests (Rowe, 1996). *C. polykomos* and *C. guereza* are larger and more dimorphic than the Asian forms, and live in the western and central/eastern regions of the central African rainforest, respectively (Fleagle, 1999). The percentage of travel time spent leaping differs between them perhaps because *C. polykomos* lives primarily in continuous, primary forest, while *C. guereza* frequents more secondary forest and wooded grassland (Rowe, 1996), where leaping between supports is more likely to be necessary.

Phylogenetically, *Colobus* and *Presbytis* are both members of the Colobinae, but belong to separate branches of the subfamily; *Presbytis* is more closely related to the 'odd nosed' colobines (*Nasalis*, *Rhinopithecus*, *Pygathrix*), while *Colobus* is part of a monophyletic African clade with *Pliocolobus* (Wang et al., 2012). In both cases, the species examined here are very closely related to their congeners, sharing a common ancestor with only one other species (*P. comata* and *C. vellerosus*,

126 respectively), aside from each other (Ting, 2008; Meyer et al., 2011).

127

128 The decision to examine congeners was taken to diminish the effect of extraneous variables on the
129 ensuing comparisons; this can be useful for detecting adaptive responses (Crews, 1997). Species
130 pairs form natural experiments from which behaviours can be linked to morphology (Fleagle, 1976,
131 1977; Katz and Harris-Warrick, 1999). For example, comparing closely related taxa has the effect
132 of reducing the influence of phylogeny, so that those differences of interest (in this case, frequency
133 of leaping) can be examined in relative isolation (Birkhead et al., 1992). Using two different
134 species pairs eliminates many of the inherent problems (Garland and Adolf, 1994) with standard
135 two-species comparisons.

136

137 Table 1 about here

138

139 Materials and methods

140

141 A mixed-sex sample of wild-shot, adult dry crania of *P. melalophus* (n = 5) and *P. potenziani* (n = 4)
142 from the collection of the Primate Research Institute of Kyoto University, Inuyama, Japan, and of
143 *C. polykomos* (n = 6) and *C. guereza* (n = 5) from the Natural History Museum, London, U.K., was
144 examined. *Colobus* individuals were scanned at Hull York Medical School using a X-TEK
145 HMX160 high-resolution computed tomography scanner (X-Tek Systems, Tring, U.K.), with no
146 additional filters applied. All scans were taken at 75 Kv and 30 µA. Voxel size was specimen-
147 dependent, but was ≤0.04mm in all cases. *Presbytis* scan sets were obtained at the Asahi University
148 School of Dentistry, Japan, using a Scan-Xmate-RB090SS (Comscan Tecno, Sagamihara, Japan).
149 All scans were acquired at 80-90 Kv and 90-100 µA, with a voxel size ≤0.04mm.

150

151 Semicircular canal parameters were determined using a modified version (Schmelzle et al. 2007) of

the methods outlined in Spoor et al. (2007). Virtual 3D models of the labyrinth (Fig. 2) were constructed via manual segmentation in Avizo ver. 8 (Visualization Sciences Group, Burlington, MA). Although other parameters of vestibular morphology have been investigated (Pfaff et al., 2015; Grohé et al., 2016), the present study focuses on the radius of curvature (R) as a measure of canal size (Schmelzle et al., 2007). R is derived from internal height and width measurements: height is measured from the protrusion of the ampulla at the lowest point of the canal to its maximum possible extent on the canal opposite, width was then determined as the maximum length line intersecting the height line at 90° (Fig. 3). R is calculated as $0.5 \times ((\text{Height} + \text{Width}) \div 2)$.

Figure 3 about here

To scale for size, values for each canal were derived by dividing R by the cranial body mass estimate prosthion–inion cranial length (Martin and Ross, 2005); previous work (Johnson, 2012) on *Colobus* shows that similar results obtain using other canal variables and scalars. The resulting data were analysed for normality, then by independent samples tests in IBM SPSS ver. 21 with $\alpha = 0.05$ for significance.

Results

Examples of the virtual reconstructions of the canals are shown in Figure 4. The mean values of R and cranial length are given in table 2. The 95% confidence intervals of the regression slopes of R against size included isometry except in the case of the anterior canal, where the lower confidence interval approached isometry. No samples of R for which $n > 5$ differed significantly from normality (the small sample of *P. potenziani* precluded analysis).

Neither species pair differed significantly in size-corrected R for anterior canals (Fig. 5). In

Presbytis, however, the species that leaps more frequently (*P. melalophos*) shows significantly larger lateral canals; t = 2.867, df = 7, Sig. (2-tailed) = 0.024. The results for *Colobus*, however, show an entirely different pattern; the leaping form (*C. guereza*) has both anterior and lateral canals that are statistically indistinguishable from its congener, but possesses posterior canals that are significantly smaller; t = -2.656, df = 10, Sig. (2-tailed) = 0.024 (Fig. 5).

Figure 4 about here

Figure 5 about here

Discussion

In *Presbytis*, the difference (larger lateral canals) between species that vary widely in the amount they leap during locomotion is in the same canal and in the same direction as that reported for other primates (Spoor et al., 2007). Combined with the fact that this statistically significant difference is found even at relatively small sample sizes (n=4-6), this could be construed as support for previous interpretations. The fact that *Colobus* species show a completely different pattern (the leaping form has smaller posterior canals), however, suggest that caution should be exercised when attempting to use the *Presbytis* results on their own to infer behaviour in extinct forms.

The failure of primate congeners that differ in specifics in the locomotor repertoire to show a consistent pattern in semicircular canal size suggests that either a) leaping reflects a sufficiently different aspect of locomotor function from the multivariate agility categories utilised previously that the morphological signals in the organ of balance are not comparable, b) increasing the amount of leaping in the locomotor repertoire by over 100% has no effect on labyrinth morphology, or c) the influence of drift at the lower taxonomic level examined here is greater than any inferred

functional adaptation. Precisely which of these possibilities is most probable is unclear at present.

Even though it had been suggested previously (Spoor et al., 2007; Walker et al., 2008) that leaping may have a critical effect on the organ of balance, the differences between the broad behavioural categories of agility used in more wide-ranging studies on the one hand and specifically leaping on the other may be sufficient to result in distinct patterns of labyrinthine morphology. As the agility scores used in previous research (e.g., Spoor et al., 2007) include speed (and, presumably, additional attributes of locomotor behaviour), it may be that these factors (rather than percentage of leaping) have affected the results. Indeed, although the larger lateral canals of tarsiers have been linked explicitly to their leaping behaviour (Spoor et al., 2007), they have also been suggested to be the result of the increased degree of head rotation associated with their vertical clinging and leaping mode of movement (Spoor and Zonneveld, 1998). If this is the case, leaping may not be a sufficiently powerful selective pressure to affect the organ of balance substantially, in which case other explanations for the significant results obtained above are necessary.

It also could be argued that the amount of difference between taxa in terms of the percentage of leaping in the locomotor repertoire recorded here (over 100% in both cases) is insufficient to affect the organ of balance. If so, then the labyrinth differs from other anatomical systems (e.g., skeletal and muscular; Fleagle, 1976, 1977) that demonstrate just such variation within the same subfamily; indeed, for one case, in the same genus. Again, however, the contradictory nature of the results complicates the interpretation, as the significant results suggest that some effect is present, but in two different directions on two different canals. It has also been demonstrated that a substantial amount of phylogenetic signal may be present in labyrinthine morphology of some primate groups (Lebrun et al., 2010), which could affect the results, although the use of congeneric pairs reduces the likelihood that this is a significant factor. In addition, because behavioural flexibility is a characteristic of primates, and because behaviour can change more quickly than morphology,

evolutionary lag might be invoked (Blomberg et al., 2003), although it would not fully account for the conflicting significant differences.

A final potential interpretation is that the differences seen are the result of genetic drift. If this is the case, it would imply that chance affects labyrinth morphology to a greater extent than forces produced during locomotion. In some ways, drift is (and perhaps should be) the null explanation for differences between closely related taxa (or, indeed, individuals); a notion that is receiving more attention recently (e.g., Weaver et al., 2007; Betti et al., 2010). Additional testing would be required to see if the pattern of the variation in semicircular canal radius in colobines is distinguishable from those derived from drift models; if not, no functional explanation for the observed differences would be necessary. Alternatively, it may be that a multivariate approach (Gunz et al., 2012) is needed to differentiate between taxa such as those investigated here, although this may limit the extent to which individual traits of the labyrinth can be subjected to statistical testing. In any event, the fact that these significant patterns are diametrically opposed in two sets of closely related taxa reduces the confidence that can be placed on inferences derived from comparisons between fossil and living taxa.

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TABLES

Table 1: Percentage of leaping in the locomotor repertoire of *Presbytis* and *Colobus*. Data derived from Fuentes (1996), Gebo and Chapman (1995), McGraw (1998) and Reed (1999). For both genera, the species indicated by an asterisk (*) leaps more than twice as frequently as its congener.

TAXON	% leaping	% quadrupedalism	% other
*Presbytis melalophos**	67.5	20.5	12
P. potenziani	25	75	0
*Colobus guereza**	38	41	21
C. polykomos	14.5	71.2	14.3

Table 2. Species means for canal radius R (mm) and the cranial size proxy (prosthion-inion length; mm)

Taxon	n	Anterior	Posterior	Lateral	Size
Presbytis melalophos	5	2.24	2.23	2.34	98.62
Presbytis potenziani	4	2.26	2.00	1.97	92.98
Colobus guereza	6	2.66	2.32	2.22	112.96
Colobus polykomos	6	2.61	2.48	2.28	109.28

418 FIGURE LEGENDS

419

420 Figure 1: Location of the bony labyrinth (shaded) in the temporal bone, seen in a 3D virtual
421 reconstruction of a *Presbytis* cranium derived from µCT scans and rendered semi-transparent.

422

423 Figure 2: 3D virtual reconstruction of the bony labyrinth of *Presbytis*. The semicircular canals are
424 orientated orthogonally to one another for sensing pitch, roll and yaw of the head. Scale bar = 1mm.

425

426 Figure 3: Height (h) and width (w) measurements used to calculate canal radius (R). Scale bar =
427 1mm.

428

429 Figure 4: Virtual canals of a) *Colobus guereza,* b) *C. polykomos* (reversed), c) *Presbytis*
430 *melalophos,* and d) *P. potenziani*. Scale bars = 1mm.

431

432 Figure 5: Box and whiskers plots of size-adjusted R of *Presbytis* and *Colobus* semicircular canals.
433 The anterior, posterior and lateral canals are indicated below each chart. The species that leaps
434 more frequently is indicated by the monkey symbol.

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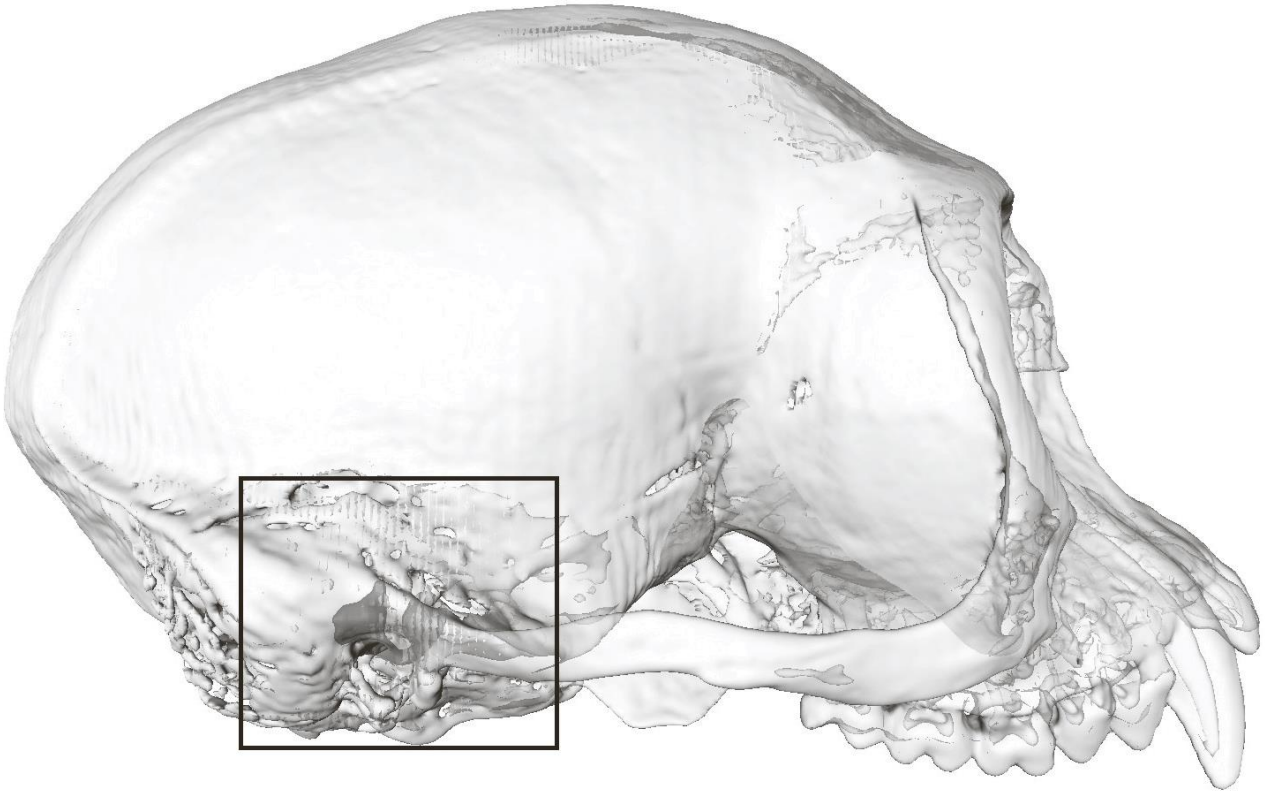

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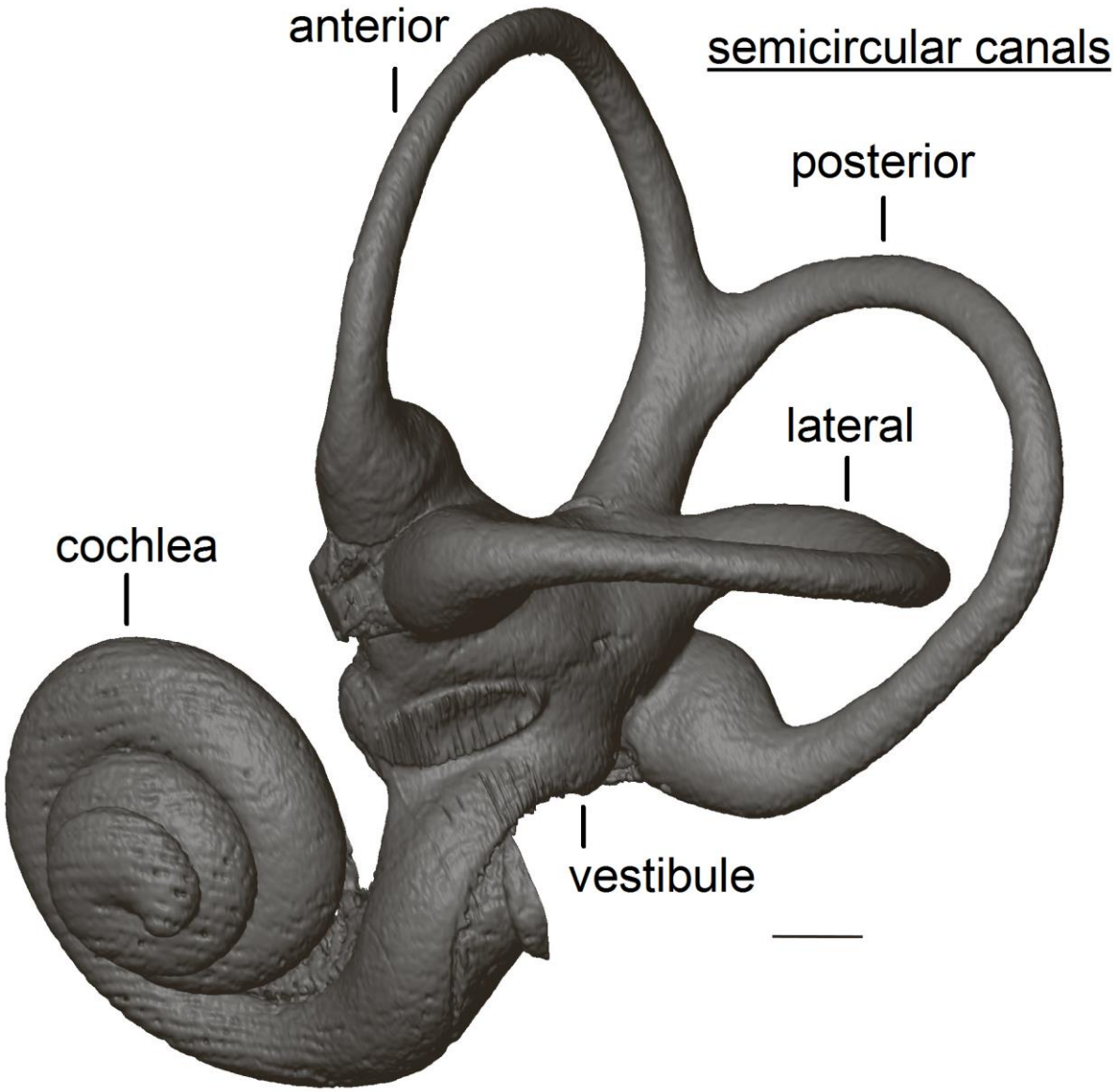
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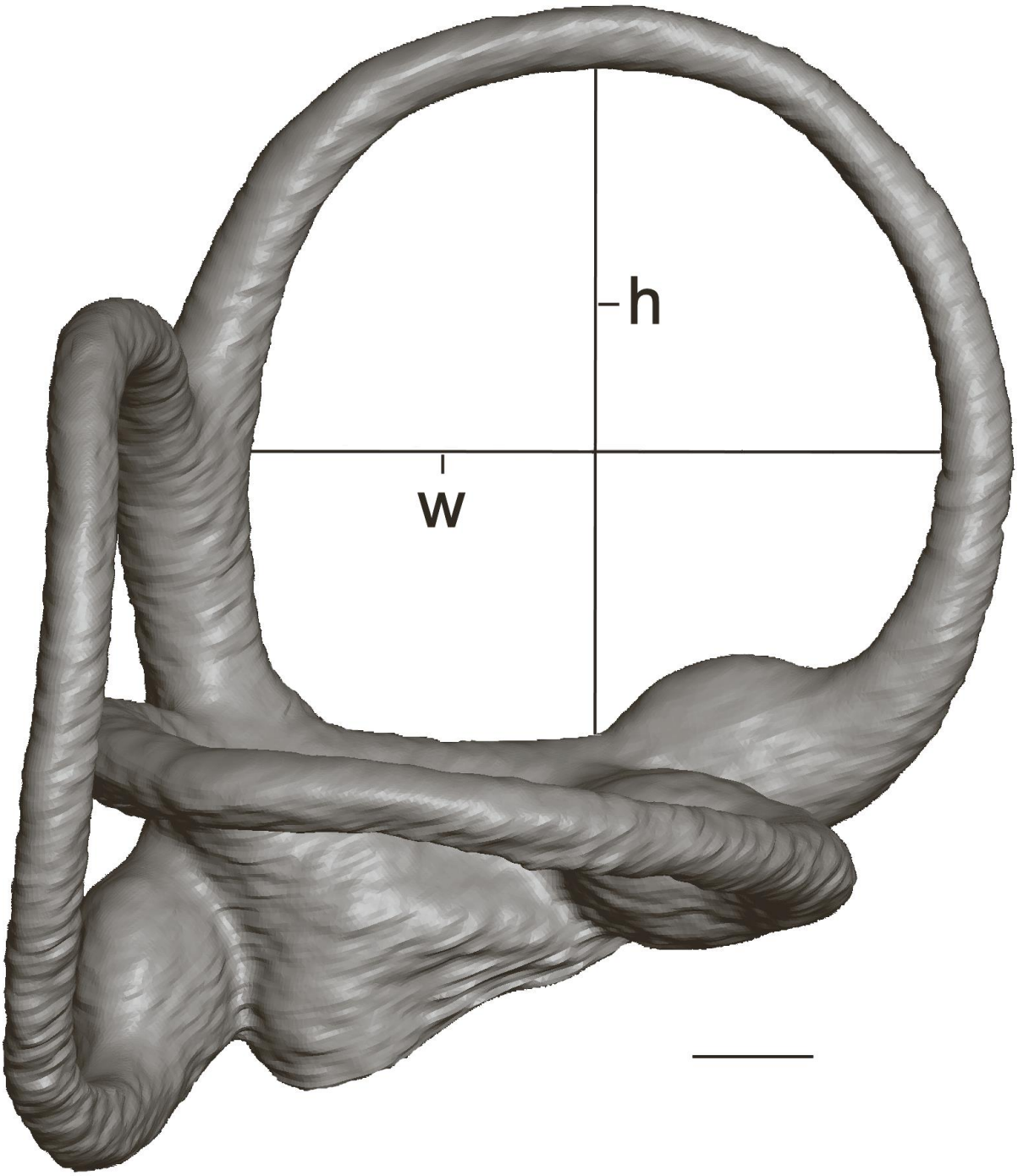

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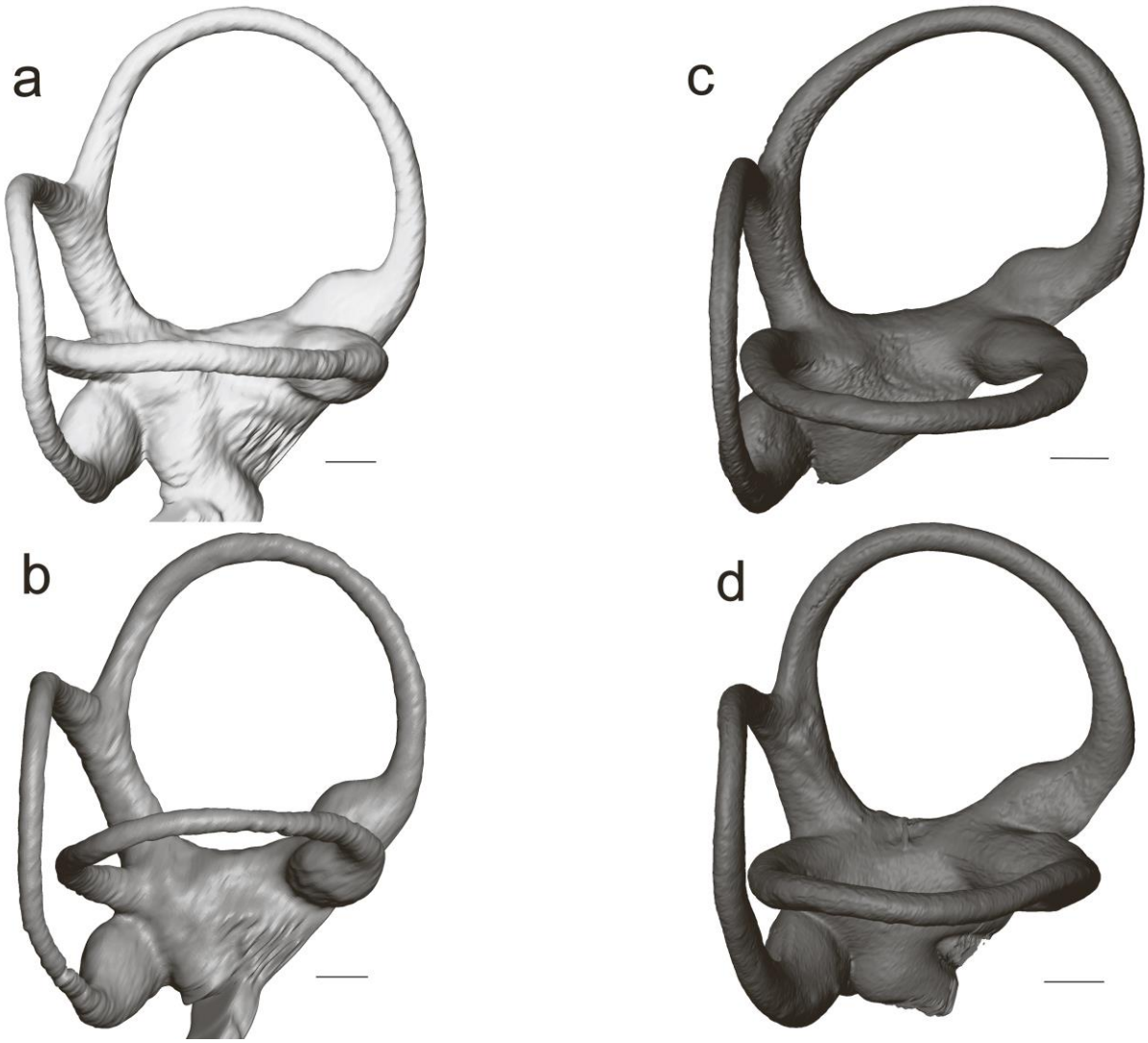

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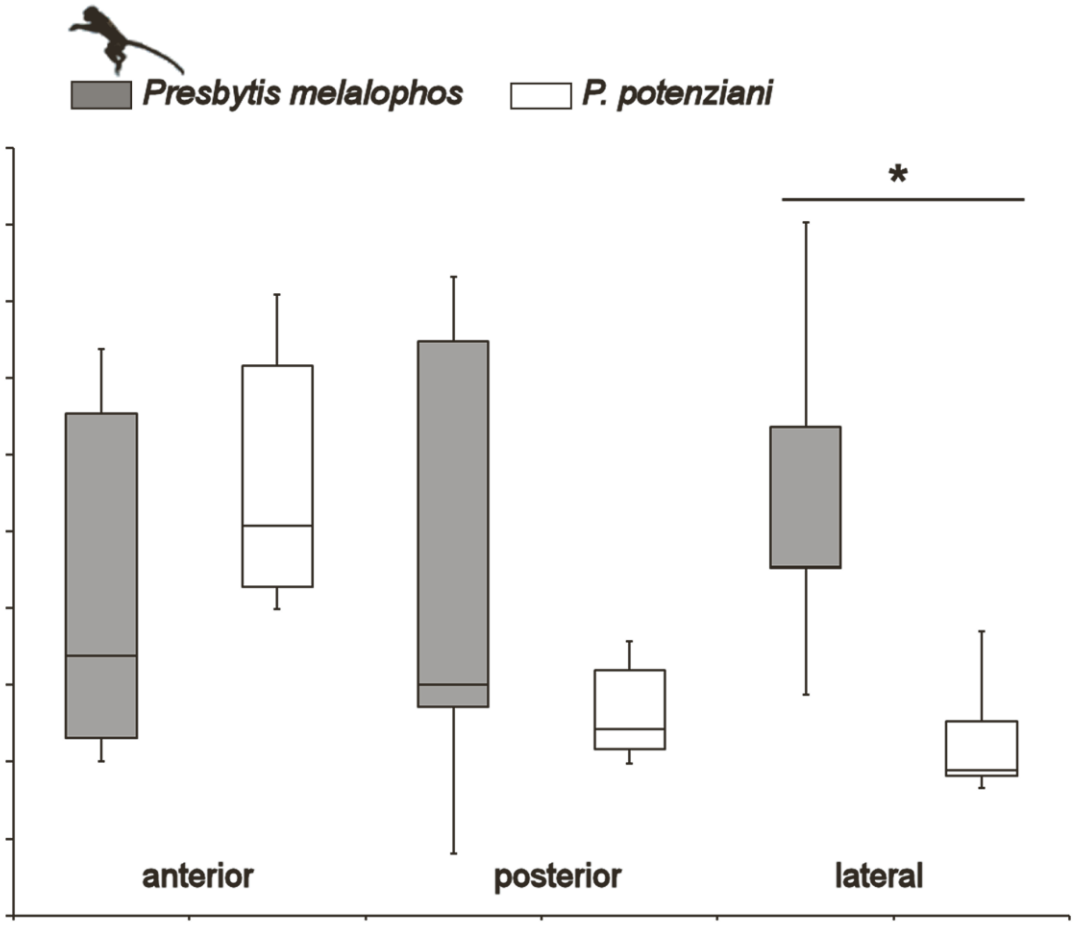
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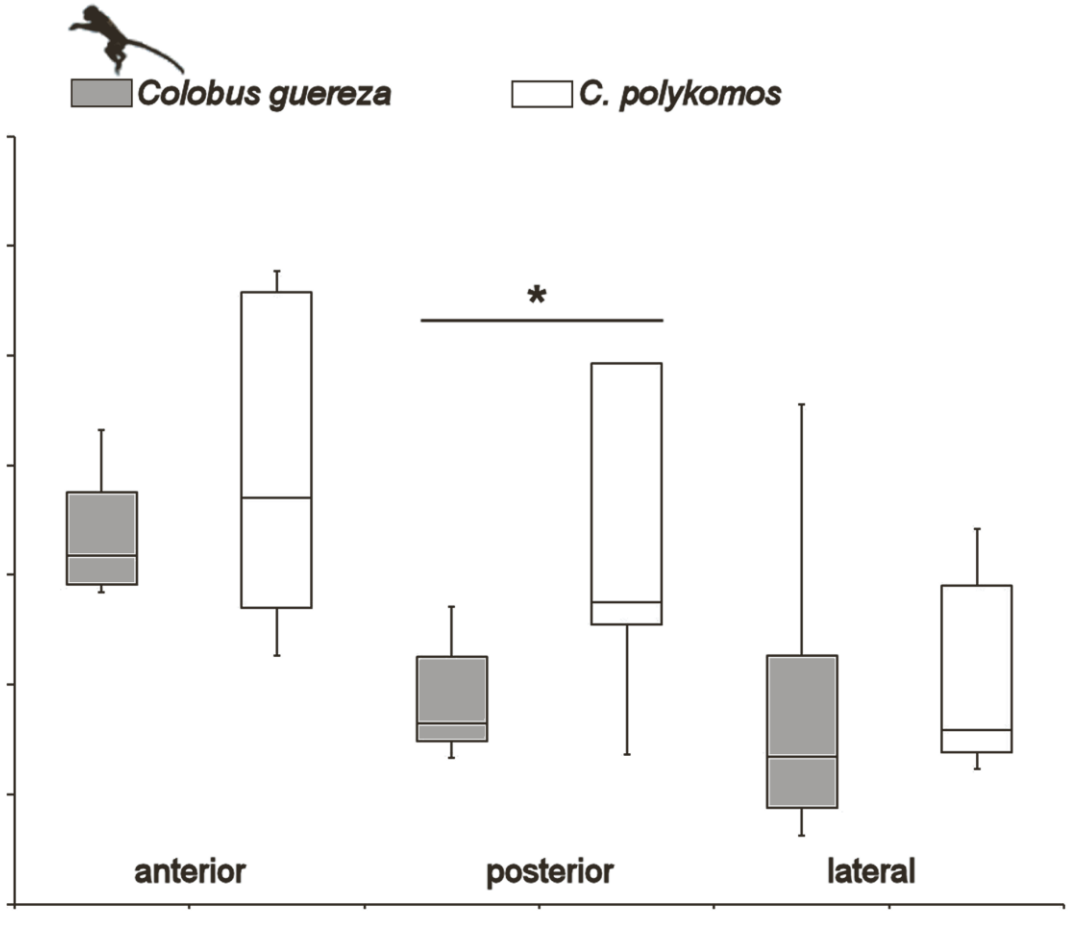
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